Local forage fish abundance influences foraging effort and offspring condition in an Endangered marine predator

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ABSTRACT

1. Understanding the functional relationship between marine predators and their prey is vital to inform ecosystem-based management. However, collecting concurrent data on predator behaviour and their prey at relevant scales is challenging. Moreover, opportunities to study these relationships in the absence of industrial fishing are extremely rare.

2. We took advantage of an experimental fisheries closure to study how local prey abundance influences foraging success and chick condition of Endangered African penguins *Spheniscus demersus* in the Benguela Ecosystem.

3. We tracked 75 chick-provisioning penguins with GPS-time-depth devices, measured body condition of 569 chicks, quantified the diet of 83 breeding penguins and conducted 12 forage fish hydro-acoustic surveys within a 20 km radius of Robben Island, South Africa, over three years (2011–2013). Commercial fishing for the penguins' main prey, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, was prohibited within this 20 km radius during the study period.

4. Local forage fish abundance explained 60% of the variation in time spent diving for 14 penguins at sea within 2 days of a hydro-acoustic survey. Penguin foraging effort (time spent diving, number of wiggles per trip, number of foraging dives and the maximum distance travelled) increased and offspring body condition decreased as forage fish abundance declined. In addition, quantile regression revealed that variation in foraging effort increased as prey abundance around the colony declined.

5. *Policy implications*. Our results demonstrate that local forage fish abundance influences seabird foraging and offspring fitness. They also highlight the potential for offspring condition and the mean-variance relationship in foraging behaviour to act as leading indicators of poor prey abundance. By rapidly indicating periods where forage resources are scarce, these metrics could help limit seabird-fisheries competition and aid the implementation of dynamic ocean management.

KEYWORDS: African penguin, Benguela ecosystem, dive behaviour, fisheries closures, forage fish, foraging ecology, marine spatial management, prey abundance.

1. INTRODUCTION

Understanding the functional relationship between predators and their prey is essential for ecosystem-based management of the oceans (Sainsbury, Punt & Smith 2000), particularly where commercial fisheries target the same forage resources. Although the effect of forage fisheries on higher trophic levels is debated, fishing can at least impact central-place foragers via localized prey depletion (Conn *et al*. 2014; Sherley *et al*. 2015, 2018). Truly understanding these impacts, however, depends on knowing how predators respond to natural changes in prey availability (Boyd *et al*. 2016; Sydeman *et al*. 2017). But because industrial fisheries pervade almost all ocean ecosystems (Halpern *et al*. 2007), we are almost never afforded the opportunity to study predator-prey dynamics in the absence of the potential confounding effect of fishing.

Seabirds are considered to be useful indicators of prey availability (e.g. Piatt *et al*. 2007; Brisson-Curadeau *et al.* 2017). Fisheries catch records (e.g. Thomas & Schülein 1988) combined with seabird at-sea counts (e.g. Davoren, Montevecchi & Anderson 2003) have been used to investigate these relationships, and the miniaturisation of tracking devices has enabled comparison of seabird movements to prey abundance using broad-scale hydro-acoustic surveys (e.g. Grémillet *et al*. 2008; Sherley *et al*. 2017). Nonetheless, studies using animal-borne loggers and concurrent hydro-acoustic surveys to sample predator behaviour and prey abundance at matching spatial and temporal scales remain rare (Bertrand *et al*. 2012; Benoit-Bird *et al*. 2013; Hays *et al*. 2016). This approach is, however, critical to understand how the movement, location and abundance of prey affects predator behaviour (Hays *et al*. 2016), including potential carry-over effects on other life-history traits, and hence to comprehend the relative impact of environmental variability and fisheries extraction (Benoit-Bird *et al*. 2013; Boyd *et al*. 2016; Sherley *et al*. 2018).

To address this gap, we undertook hydro-acoustic surveys of forage fish density around Robben Island, South Africa, and concurrently deployed GPS-time-depth recorders on breeding African penguins *Spheniscus demersus*, sampled the diet of birds returning to the colony and monitored offspring body condition. African penguins are an excellent species for which to study fine-scale predator-prey interactions. Their foraging range when breeding is more restricted than seabirds which fly (Pichegru *et al*. 2009), offering a tractable area in which to undertake hydro-acoustic surveys; chick-rearing penguins target forage fish almost exclusively (predominately young-of-the-year anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*; Crawford *et al*. 2011)*;* the core feeding zones around their colonies have been clearly delineated (Pichegru *et al*. 2009, 2013); and they do not switch to feed on fisheries waste when forage fish abundance is low (Crawford *et al*. 2011). Furthermore, concerns that breeding African penguins are in direct competition with commercial fisheries for forage fish resources led to an experimental fishing closure being implemented around Robben Island, South Africa (Sherley *et al*. 2015, 2018). Commercial fishing for the penguins' main prey, anchovy and sardine, was prohibited within a 20 km radius around the island from 2011 to 2013, and both chick survival and body condition improved (Sherley *et al*. 2015, 2018). This closure provided a unique opportunity to gather valuable baseline data on how local prey abundance influenced foraging behaviour and chick condition of this Endangered penguin species in the absence of the potential confounding effects of localised fishing. Accordingly, we tested the assumption, usually implicit in studies of seabird ecology, that greater energetic and temporal investment in foraging and poorer offspring condition result directly from reduced prey abundance around the focal colony. We examine our findings in the context of developing leading indicators of how prey abundance affects predator performance, and discuss their implications for fisheries and dynamic ocean management.

2. MATERIALS AND METHODS

2.1 Data collection

We collected data at Robben Island (33°48'S, 18°22'E), South Africa, during African penguin breeding seasons (March to September) in 2011, 2012 and 2013. Robben Island was the fourth largest African penguin colony at the time, with ~1,600 breeding pairs (Sherley *et al*. 2015). In these years, a 20 km purse-seine fishing closure was in place around the island (Fig. 1); this negated the local effect of fishing sufficiently to improve chick survival and body condition (Sherley *et al.* 2015, 2018). Fishing continued outside this 20 km area.

2.1.1 Forage fish hydro-acoustic surveys

We conducted hydro-acoustic surveys within a 20 km radius around the island ('small-scale surveys') from a rigid-inflatable boat using a scientifically-calibrated SIMRAD EK60 echo-sounder comprising a pole-mounted ES38-12 split beam transducer and console-housed general-purpose transceiver (Merkle, Coetzee, Mushanaganyisi & Rademan 2012a; Merkle, Coetzee & Rademan 2012b). The two-day surveys followed transects perpendicular to the mainland (Fig. 1C), were carried out during daylight (when the penguins predominantly forage, Wilson & Wilson 1990) and were scheduled (Fig. 2, Table S1) as logistics and weather allowed. The surveys started north of the island and ran southwards, except in June 2011 when the survey was reversed for logistical reasons. The survey area coincided with the penguins' foraging range (Wilson 1985; Pichegru *et al*. 2009).

To contextualise our small-scale biomass estimates, given that annual conditions vary substantially in this ecosystem, we also obtained broad-scale information on the abundance of anchovy and sardine recruits from annual large-scale hydro-acoustic surveys of forage fish recruitment conducted over a distance > 1,400 km along the South African coastline in May–June each year for stock assessment purposes (Coetzee *et al.* 2008; de Moor, Butterworth & Coetzee 2008). We took estimates from the survey section containing Robben Island (Stratum D, Cape Columbine to Cape Point; de Moor *et al*. 2008). The small-scale surveys covered < 400 km^2 while the large-scale surveys covered > 150,000 km^2.

2.1.2 Device deployments

Between April and August each study year, we equipped one adult from pairs of African penguins rearing small chicks with GPS-temperature-depth loggers for one foraging trip per breeding season following recommended methods for deployment on diving birds. No bird was tracked more than once per season. Wherever feasible, deployments were timed to coincide with the small-scale hydro-acoustic surveys (Fig. 2). Appendix S1 contains detailed methods.

2.1.3 Chick measurements

Chicks were captured by hand, measured for head length (tip of the bill to back of the skull; ± 0.1 mm) using Vernier calipers, and weighed for mass (± 10 g) using electronic balances and cloth bags to hold the chicks. We sampled in two of the four weeks each month from March in all years and until October in 2011, until September in 2012 and until August in 2013. Nests were marked to ensure that chicks were not measured more than once per season and we made efforts to sample chicks from different areas in the colony equally each year.

2.1.4. Diet samples

A random sample of adult birds in transit back to their nests on Robben Island has been periodically sampled for diet using the water-offloading technique since 1989 (Wilson 1984, Crawford *et al*. 2011). Diet samples for 2011, 2012 and 2013 were sorted into principal prey items and weighed to obtain percentage mass of different prey species within each sample.

2.2 Analysis

2.2.1 Hydro-acoustic survey data

Nautical Area Backscattering Coefficients (NASC, m^2 nmi^{-2}) derived from integration of mean volume backscattering strength data (S_v, dB re $1m^2$ m^{-3}) originating from forage fish were integrated over the upper 50 m of the water column for 2.5 nautical mile sections of transects (Elementary sampling distance unit; ESDU) using Myriax Echoview©. Mean forage fish area densities ($\bar{\rho}_i$, kg m^{-2}) were derived as:

$$\bar{\rho}_i = \frac{NASC_i}{4\pi(1852)^2 10^{\frac{\overline{TS}_{kg}}{10}}}$$

(eqn. 1)

for each ESDU i, by applying the anchovy weight-normalised target strength (dB kg^{-1}), where $\overline{TS}_{kg} = -12.15 log L_t - 21.12$ (Barange, Hampton & Soule 1996, Coetzee *et al*. 2008, Merkle *et al*. 2012a, 2012b), and were averaged per transect and for the survey area following Jolly & Hampton (1990). Total forage fish abundance (tonnes) was calculated by extrapolating the mean survey forage fish density to the total area surveyed (km^2). In the large-scale surveys, catch composition and length frequency distributions from concurrent trawl samples were used to distinguish between anchovy and sardine (Coetzee *et al*. 2008). For the small-scale surveys, however, we could not distinguish fish to species level, although catches taken within 30 nautical miles (55.6 km) of the island (but outside the 20 km closure zone) and during the large-scale recruitment surveys of 2011–2013 indicated that anchovy was dominant (Coetzee 2014). Given that African penguins predominantly forage in the upper 50 m of the water column (Wilson & Wilson 1990; Pichegru *et al.* 2013), the small-scale survey biomass estimates were calculated by excluding all recordings of fish at a depth in excess of 50 m (Merkle *et al*. 2012b) and thus represent forage fish biomass within the foraging range of penguins.

2.2.2 Foraging behaviour

African penguins alternate periods of traveling underwater and at the surface (Wilson 1985). We considered depths >1 m to indicate diving and depths > 3 m as foraging dives (Wilson & Wilson 1990; Pichegru *et al.* 2013). For each foraging trip, we calculated six indices to describe foraging effort: (1) trip duration (total time spent on the foraging trip, h), (2) maximum distance travelled (furthest straight-line distance from the colony, km), (3) time spent diving (h), (4) number of foraging dives (dives >3 m), (5) number of wiggles (estimates of prey pursuit and/or capture, see e.g. Sala, Wilson & Quintana 2012), and (6) prey-pursuit per unit effort (PPUE;

189 wiggles.min^{-1}). See Appendix S1 for detailed methods and definitions of the six foraging effort
190 indices.
191
192 **2.2.3 Chick condition**
193 For chicks with head lengths >75 mm, we estimated body condition using a species-specific
194 index based on regressing mass against head length using data from a cohort of 125 chicks
195 that survived to fledging on Robben Island in 2004 (Lubbe *et al.* 2014; see Appendix S2). To
196 extend this to smaller chicks (generally ≤20 days old), we fitted 840 weighted quantile
197 regressions for each 0.1 mm of chick head length to the same data. This yielded a non-linear
198 body condition index (BCI) for head lengths from 38.0 mm to 122.0 mm by 0.1 mm for the
199 entire data set (Fig. S2, see Appendix S2 for details). We then calculated a BCI value for each
200 chick measured during 2011 to 2013.
201
202 **2.2.4 Relationships between local prey abundance, chick condition, diet composition,**
203 **and foraging behaviour**
204 We examined how penguin foraging behaviour responded to forage fish biomass around the
205 island in two ways. First, we compared the six foraging effort indices between a relatively large
206 (2012) and small local forage fish biomass year (2011) for all the penguins tracked in these
207 years. Secondly, we investigated the relationship between each index and the individual
208 abundance estimates from the hydro-acoustic surveys using data from penguins that had
209 been tracked within two days of each survey. This temporal window was based on
210 consideration of forage fish swimming speeds (Appendix S3). Annual sample sizes at this
211 temporal window were small, so data from all years were combined. Relationships between
212 the six foraging parameters and local prey biomass were investigated using linear regression
213 and quantile regression ('rq' function, 'quantreg' package for R). We then checked to ensure
214 that any significant effects were robust using Pearson's correlation on ranks (Zar 1999) for
215 both the individual data and the means for each survey (see Appendix S4).

We used Gaussian linear mixed-effects models ('lme' function, 'nlme' package for R) to model the relationship between chick BCI (response) and the local forage fish biomass (continuous covariate) using measurements within 14 days of each small-scale survey following Waller (2011). We used AICc values and restricted maximum likelihood (REML) estimation to compare between four alternative structures for the random effects (year, month nested in year, survey, and survey nested in year, see Table S2); the basic model structure took the form:

$$y_{i,j} = \beta_1 + \beta_2 x_{i,j} + \omega_i + \varepsilon_{i,j}, \qquad i = 1, \ldots 10, \qquad \omega_i \sim N(0, \sigma^2), \qquad \varepsilon \sim N(0, \sigma^2)$$

(eqn. 2)

where $y_{i,j}$ is the jth observation of chick body condition (BCI), $x_{i,j}$ is the forage fish abundance estimate made during small-scale survey i and ω_i is the random intercept. Two models were equally well supported (see Table S2), so we used model model-averaged coefficients based on REML estimation (Zuur *et al.* 2009) from these two models and generated estimates for plots using the 'model.avg' function ('MuMIn' package for R). Plots of the model residuals were examined to check the assumptions of normality and homogeneity of variance. Non-parametric tests were used where appropriate.

3. RESULTS

3.1 Variation in local forage fish abundance

Twelve small-scale hydro-acoustic surveys were conducted, six in 2011, five in 2012 and one in 2013 (Fig. 2, Table S1); the mean ± SE of forage fish biomass was 50,915 ± 17,887 t. However, this varied by more than two orders of magnitude (range: 549–187,249 t; Fig. 2, Table S1). The median abundance in 2011 (5,981 t) was about 8% of the median abundance in 2012 (72,711 t; Fig. 2). Similarly, the combined recruitment biomass of anchovy and sardine from the large-scale survey was 12,333 t in 2011, or 13% of the 92,725 t estimated for 2012. In 2013, only one small-scale survey was conducted; forage fish abundance around the island

in May was 7,159 t (Fig. 2), about 10% of the 2012 median, while the large-scale survey (also conducted in May) recruitment biomass was 460,430 t (~5 times higher than 2012).

3.2 Foraging behaviour

We collected 30,171 dive records from 75 penguins, of which 252 (0.8%) were deeper than 50 m. With the exception of PPUE, all indices of foraging effort were significantly greater in 2011, when prey was less abundant, than in 2012 (Table 1). The number of wiggles in a trip and the total time a penguin spent diving were positively correlated (r_s = 0.74, S = 17233, N = 74, p <0.001), although heteroscedasticity in the number of wiggles increased with increasing time diving (Fig. S3).

In total, 14 penguins were tracked within two days of a survey. Four indices showed strong relationships with the local forage fish abundance: the time spent diving (linear regression: r = −0.79, $F_{1,12}$ = 19.86, p <0.001; Fig. 3A), the total number of wiggles per trip (r = −0.70, $F_{1,12}$ = 11.43, p = 0.005; Fig. 3B), the number of foraging dives (r = −0.63, $F_{1,12}$ = 7.87, p = 0.016) and the maximum distance travelled (r = −0.58, $F_{1,12}$ = 5.93, p = 0.031; Fig. 3C) were negatively related to the forage fish biomass. In particular, the local prey abundance explained more than half of the variation in the time the penguins spent diving (adjusted R^2 = 0.60). However, the data showed heteroscedasticity, and the 10% and 90% quantile regression lines indicated that the variance in both the maximum distance travelled and the number of wiggles increased as forage fish biomass decreased (Fig. 3).

3.3 Chick condition

Two models with different random effect structures ('survey' and 'month nested in year') had similar AICc support (Table S2), so model averaging was performed across these models. Chick body condition (N = 569) significantly increased with the abundance of forage fish around the island (model averaged coefficient estimate = 0.00152 change in condition per t x 10^3, z = 2.41, p = 0.017; Fig. 4). The predicted increase in chick body condition was 174%

269 over the observed range of fish abundance of 186.7 x 10^3 t, from 0.164 (95% CI: 0.045–0.282)
270 at the smallest observed biomass to 0.449 (0.334–0.563) at the largest (Fig. 4).
271
272 **3.4 Diet composition and foraging behaviour**
273 Anchovy mass contributions in the penguin diet were 36% in 2011 (N = 44), 97% in
274 2012 (N = 15) and 93% in 2013 (N = 24) (Table S3). To control for the effect on foraging
275 behaviour that these differences in diet composition might have, we compared our foraging
276 indices between two periods when the small-scale surveys detected a relatively large and a
277 small local biomass of prey using 2012 data only (N = 20 penguin trips). In April, when the
278 local biomass was 72,711 t, the penguins travelled on average 2.3 km (95% CI: 0.1–4.5 km)
279 farther from the island (Welch's *t*-test: $t_{5.26}$ = 2.70, p = 0.04) and made 189 (95% CI: 37–341)
280 more foraging dives on average (Welch's *t*-test: $t_{3.33}$ = 3.75, p = 0.03) than they did in July
281 when the biomass was 159,039 t. The other foraging effort indices did not differ (p >0.05).
282
283 **4. DISCUSSION**
284 Since Cairns (1987) first proposed using seabird performance to assess food supply in the
285 ocean, hundreds of studies have tested for such a relationship (Brisson-Curadeau *et al.* 2017).
286 Most suffer from mismatches in the temporal and spatial resolutions of predator and prey
287 information because the fisheries data and stock assessment outputs typically used do not
288 measure prey abundance at scales relevant to seabirds (but see Grémillet *et al.* 2004; Durant
289 *et al*. 2010; Bertrand *et al*. 2012; Benoit-Bird *et al.* 2013). Here, by combining tracking data,
290 colony-based sampling and concurrent hydro-acoustic surveys, we demonstrate empirically
291 that the abundance of prey within the core foraging range of a central-place forager dictates
292 changes in both foraging effort and offspring fitness.
293 Although our sample size used to link foraging effort directly to prey abundance was
294 modest (N = 14) as a result of strictly matching surveys and bird behaviour on temporal scales
295 (see Appendix S3), a number of lines of evidence support the premise that the penguins
296 adjusted their behaviour in direct response to prey abundance (Fig. 3). Firstly, the response

297 in offspring condition (N = 569) across a change in local biomass in excess of two orders of
298 magnitude accorded directly with this conclusion (Fig. 4). Secondly, the penguins travelled
299 farther and spent more time diving for prey in 2011, than in 2012 (N = 64, Table 1 and S3). In
300 addition, they showed an increase in pursuit behaviour (wiggles) when their preferred prey
301 was at lower local abundance in 2011, and apparently harder for them to access (based on
302 diet sampling). And thirdly, the comparison made within 2012, when anchovy recruits
303 dominated the penguins' diet, conformed to the same overall pattern. Moreover, these findings
304 are consistent with the literature: in years with less prey abundance seabird provisioning trips
305 are longer, cover greater distances, and consist of longer times diving (e.g. Burger & Piatt
306 1990; Monaghan *et al*. 1994).

307 Two results were, however, particularly noteworthy. First, the number of wiggles
308 increased, but chick body condition decreased as prey abundance declined (Fig. 3B and 4).
309 This initially appears counter-intuitive if, as has been suggested, you take wiggles to represent
310 the number of prey captured (Sala *et al*. 2012). However, the number of wiggles does not
311 reflect, by themselves, the abundance of food as the number of prey consumed is strongly
312 associated with the size and type of prey, and not all pursuits are successful (Sala *et al*. 2012).
313 Both the combined abundance of sardine and anchovy and the percentages of anchovy in the
314 diet were smaller in 2011 than 2012 (Fig. 2, Table S1 and S3). Cape horse mackerel *Trachurus*
315 *capensis* dominated the diet in 2011 (Table S3). These fish have a poorer energy content
316 (5.65 kJ g^{-1}) than anchovy (6.03 kJ g^{-1}) or sardine (6.59 kJ g^{-1}; Balmelli & Wickens 1994), and
317 the horse mackerel in stratum D in the May 2011 large-scale survey were smaller (modal total
318 length of 5 cm) than the anchovy in the same area (modal total length of 8 cm; JCC unpubl.
319 data). Under these conditions the penguins would have needed to capture more individual fish
320 to balance their energy budgets. Moreover, the within-year comparison at times of similarly
321 high compositions of anchovy in the diet found a similar number of wiggles. Though this
322 observation of a typically specialist seabird prey-switching at weak abundance of their
323 preferred prey is not unusual (Burger & Piatt 1990), poor quality or availability of prey can

have profound population-level effects in the long-term (Ludynia *et al*. 2010; Sherley *et al*. 2017).

The second remarkable finding was the heteroscedasticity in the behavioural responses as forage fish abundance declined (Fig. 3). The apparent variation in foraging effort could be due to individual differences (Patrick *et al*. 2014), with birds exhibiting a wide range of foraging strategies when prey abundance is poor, or different prey types requiring different pursuits times underwater and changes in diving behaviour (Elliott *et al*. 2008). For penguins, this could result in longer periods underwater, making it harder to maintain cohesive foraging groups than when prey is abundant, which in turn reduces foraging efficiency (McInnes *et al*. 2017). We still have much to learn about predator-prey dynamics and replicating our approach elsewhere could provide valuable insights into exactly how and when fisheries targeting forage fish compete with threatened marine predators (Sydeman *et al.* 2017). Improvements in high-resolution multi-beam sonar (e.g. Brierley & Cox 2015) and in tracking technology, not least the continued miniaturisation of animal-borne cameras and accelerometers, will help to clarify how individuals differ in prey capture and energy expenditure in response to changing prey abundance and availability in future (Elliott *et al*. 2012; McInnes *et al*. 2017).

In the context of managing fisheries close to threatened predator populations, the natural variability of forage fish populations is often overlooked (Hilborn *et al*. 2017). The hydro-acoustic surveys in our study found high variability in the abundance of forage fish within 20 km of Robben Island both within and between years, even in the absence of local fishing activity. Indeed, it appears that we sampled across disparate ecosystem conditions; the contribution of anchovy to the penguin diet in 2011 (36%) was the poorest recorded since 1989 (Crawford *et al*. 2011), but returned to previously observed levels in 2012 and 2013. If similar studies can be undertaken using fisheries closures (or off-seasons) and small-scale hydro-acoustic surveys together over many years (to capture as much system variability as possible), they could help to determine base-line or ‘true’ functional relationships between predators and their prey (Sydeman *et al*. 2017). Similarly, if these studies sample during both phases of experimental fisheries closures, it would be possible to assess directly how these

functional relationships change in the presence and absence of fishing on a scale relevant to the foraging range of predators (Frederiksen *et al*. 2004). The distribution or spatial availability of prey to predators may well be more important that their overall abundance (Sydeman *et al*. 2017, Hilborn *et al*. 2017), thus an approach of the kind outlined here could ultimately disentangle the relative impacts of fishing and our changing climate on predator populations (Sydeman *et al*. 2017; Sherley *et al.* 2018). As a specific example, our results on chick BCI show a change, in the absence of localised fishing activity, of 174% over the range of prey abundance observed. By comparison, suspending fishing at this same colony resulted in an improvement of chick BCI of 45% once changing prey biomass had been accounted for (Sherley *et al*. 2018), or about ~26% of the variability due to local prey abundance alone. While these two studies together reinforce the importance of considering the natural variability of forage fish populations (e,g. Hilborn *et al*. 2017), they also highlight that there will be situations where the role that forage fisheries play in depleting prey resources available to threatened marine predators is not insignificant (Sherley *et al*. 2018).

In addition, the small sample size notwithstanding, our finding of increased variance in foraging effort at low prey biomass gives rise to the interesting notion that mean-variance relationships, an often overlooked driver of population structure in ecology (Benedetti-Cecchi 2003), might be useful metrics to consider in the management of forage resources. Time periods or situations where the variance in predator responses rapidly increases above some base-line level could indicate poor ecosystem states, and be used to guide management in the manner suggested for thresholds in mean responses (Cury *et al*. 2011). This remains to be seen and would require more validation. However, since it is likely inter-individual variation in foraging strategies, and so success, that ultimately drives population-level change (Courbin *et al*. 2018), a greater consideration of the importance of mean-variance relationships could have substantial impact on applied marine ecology, particularly as our oceans become more variable under climate change (Oliver *et al*. 2018).

Finally, our results suggest body condition and the variance in foraging performance as potential leading indicators for dynamic ocean management (e.g. Maxwell *et al.* 2015). The

ability to rapidly adjust, open, or close no-take zones has obvious benefits for policy makers, as it can help reduce impacts on local fisheries while maintaining ecologically relevant protection; however, the approach, requires near-real time, informative ecological data (Maxwell *et al.* 2015). Continuously collecting near-real time data on forage fish abundance is likely to prove prohibitively costly in the short term, although this may change with improvements in remote sensing and autonomous vehicles (Swart *et al*. 2016). However, for seabirds at least, body condition can be quickly assessed for a large number of individuals (Lubbe *et al*. 2014), responds quickly to changing environmental conditions (Waller 2011), appears sensitive to fisheries impacts (Sherley *et al*. 2018) and is likely to be a good leading indicator of changes in the components of population dynamics (e.g. survival) before they occur (Lewis *et al*. 2006). A similar suggestion has been made for foraging behaviour (Lewis *et al*. 2006), and we propose that future studies consider the possibility that sudden increases in the variance in predator foraging performance might be a useful, hitherto overlooked, leading indicator of marine ecosystem variability and anthropogenic change.

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AUTHOURS' CONTRIBUTIONS

K.J.C., R.B.S., A.S., L.G.U. and J.C.C. conceived the ideas and designed methodology; K.J.C., A.S., R.B.S., K.L., J.C.C., D.M., J.R., B.M.D., L.U. and A.B.M. collected the data; J.C.C. and D.G. analysed the hydro-acoustic data; B.M.D. and L.U. analysed the diet samples; K.J.C. collated the penguin data; K.J.C., L.G.U. and R.B.S. undertook the statistical analysis; K.J.C. and R.B.S. made the figures; K.J.C. and R.B.S. wrote the first draft. All authors contributed critically to revisions and gave final approval for publication.

DATA ACCESSIBILITY

All data will be archived in the Dryad Digital Repository and BirdLife Seabird Tracking Database.

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TABLES

Table 1. Comparison of six foraging parameters used to index foraging effort for 64 African penguins provisioning small chicks at Robben Island during years of relatively low (2011) and high (2012) forage fish abundance.

	Relative forage fish abundance			
	Low biomass	**High biomass**		
Foraging parameters	**2011**	**2012**		
	Mean ± SE (range); N	**Mean ± SE (range); N**	**Mean difference (95% CI)**	**Welch's t-test**
Trip duration (h)	16.2 ± 3.3 (8.7−42.9); 27	10.9 ± 1.0 (7.4−25.4); 37	5.3 (1.1−9.6)	$t_{29.3}$ = 2.6, p = 0.014
Maximum distance (km)	15.5 ± 3.3 (6.0−47.7); 25	8.9 ± 0.9 (3.8−15.5); 35	6.6 (2.1−11.0)	$t_{25.1}$ = 3.0, p = 0.006
Time diving (h)	7.1 ± 0.9 (3.3−13.5); 26	4.4 ± 0.3 (1.9−5.9); 37	2.7 (1.6−3.9)	$t_{29.3}$ = 4.7, p < 0.001
No. Foraging dives (> 3 m)	411 ± 52 (216−894); 26	256 ± 26 (106−497); 37	155 (84−227)	$t_{33.8}$ = 4.4, p < 0.001
No. wiggles	267 ± 39 (52−752); 26	104 ± 10 (25−258); 37	163 (79−247)	$t_{28.4}$ = 4.0, p < 0.001
PPUE (wiggles.min^{-1})	1.7 ± 0.2 (0.5−3.7); 26	1.5 ± 0.1 (0.4 − 2.9); 37	0.2 (−0.09−0.65)	$t_{47.8}$ = 1.5, p = 0.130

Notes: PPUE = prey-pursuit per unit effort (number of wiggles per minute in the bottom phase of dives). See Appendix S1 for definitions of the six foraging effort indices. Sample sizes (N) differ within years for the different foraging parameters because of device failure or incomplete sampling (see Appendix S1).

FIGURES

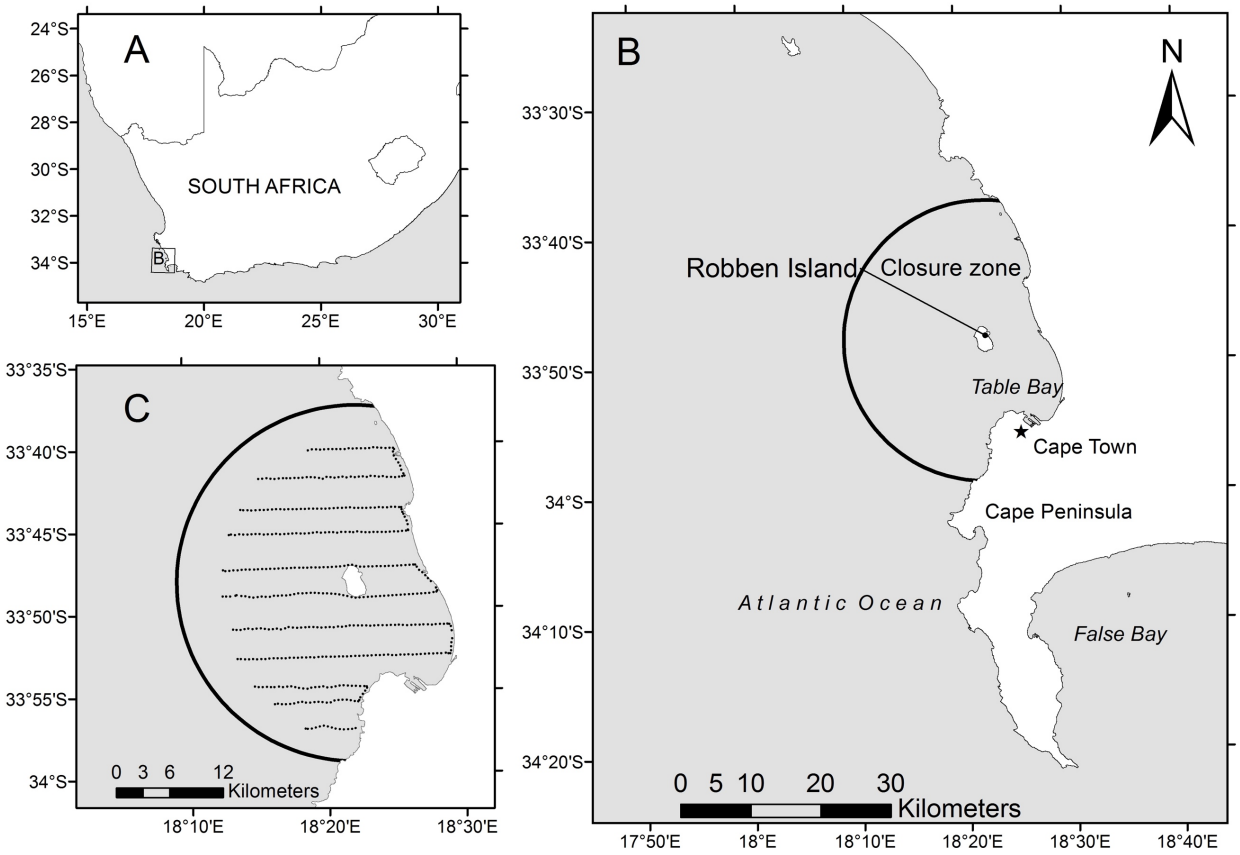

Figure 1. Maps of (A) the location of Robben Island in South Africa, (B) the 20 km radius fisheries closure zone (solid black line), and (C) the fine-scale hydro-acoustic survey transects around Robben Island (dotted lines). The transect lines were < 5 km apart.

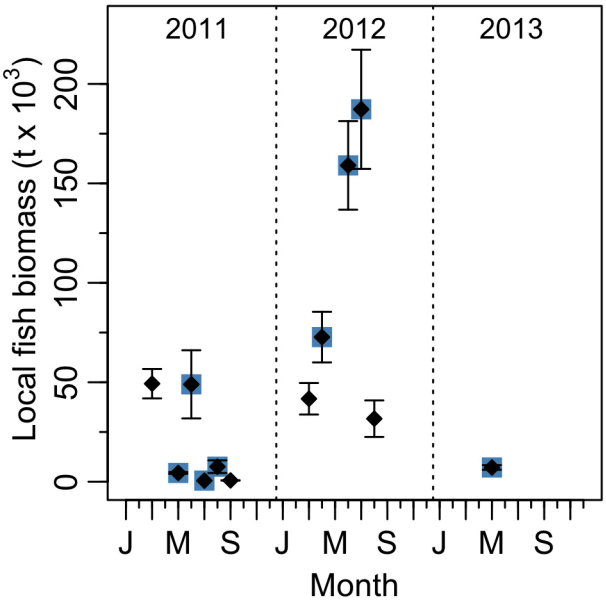

Figure 2. Forage fish biomass estimates (black diamonds) within 20 km of Robben Island from small-scale hydro-acoustic surveys conducted in 2011, 2012 and 2013, along with the times when African penguin tracking took place simultaneously (blue squares). Error bars show mean × coefficient of variation.

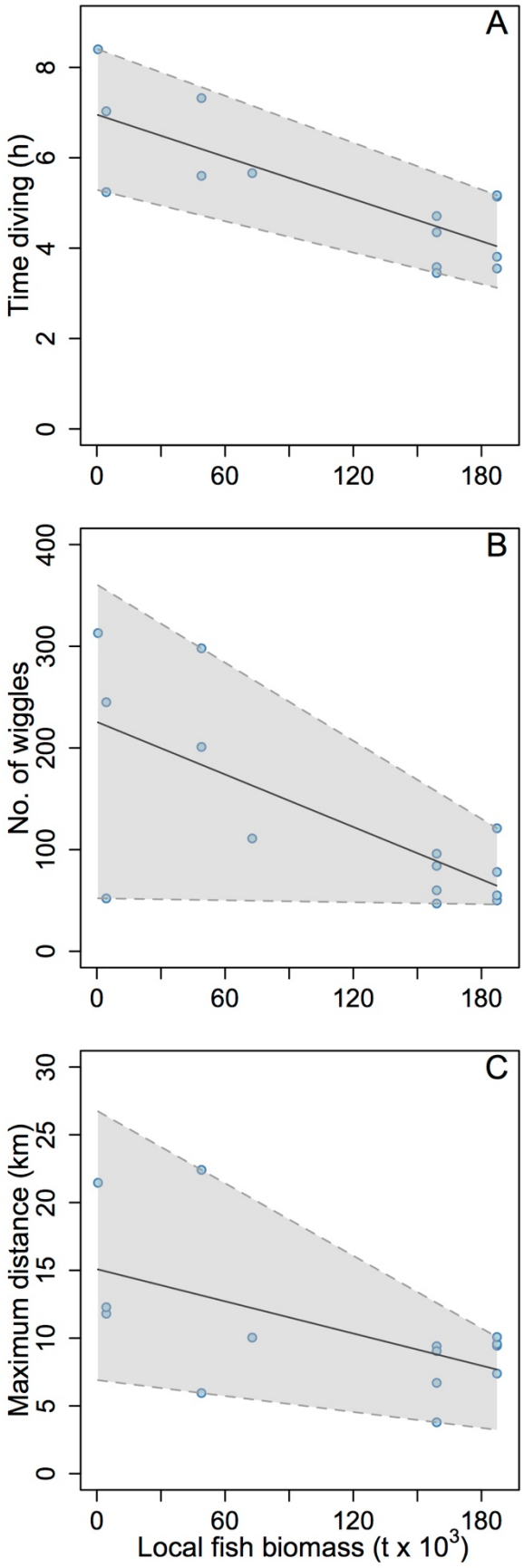

Figure 3. Estimates of African penguin foraging effort indices for 14 breeding adults related to forage fish abundance around Robben Island (tonnes x 10^3) from six hydro-acoustic surveys. The penguins were at sea within two days or less of a survey. The solid lines show the linear regression fit, the grey dashed lines show the 90% and 10% quantile lines for (A) time diving, (B) the number of wiggles per trip and (C) maximum foraging distance.

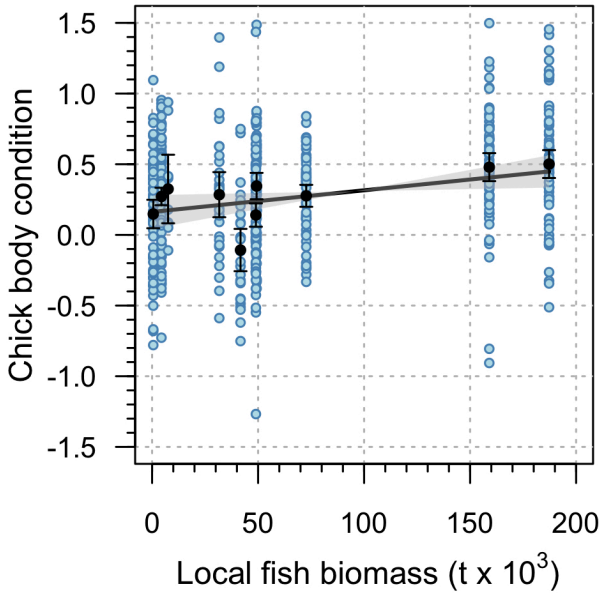

Figure 4. African penguin chick body condition (N = 569) at Robben Island in relation to forage fish abundance in a 20 km radius around the island, from 10 hydro-acoustic surveys between 2011 and 2013. The black line shows the linear mixed effects model fit with the 95% confidence intervals (grey polygon) based on model-averaged coefficient estimates from the two best supported models (Table S2). The chick body condition mean ± 95% confidence intervals (black points and error bars) for each fish survey are plotted over the data points for the individual chicks.